Illuminating symbiosis and the trading strategies of arbuscular mycorrhizal fungi

van 't Padje, A.

2020

document version
Publisher's PDF, also known as Version of record

CHAPTER 3

Finding fungal ecological strategies: Is recycling an option?

Amy Zanne, Jeff Powell, Habacuc Flores-Moreno, E. Toby Kiers, Anouk van 't Padje, and William K. Cornwell

In Press in *Fungal Ecology*

Abstract

High-throughput sequencing (e.g., amplicon and shotgun) has provided new insight into the diversity and distribution of fungi around the globe, but developing a framework to understand this diversity has proved challenging. Here we review key ecological strategy theories developed for macro-organisms and discuss ways that they can be applied to fungi. We suggest that while certain elements may be applied, an easy translation does not exist. Particular aspects of fungal ecology, such as body size and growth architecture, which are critical to many existing strategy schemes, as well as guild shifting, need special consideration in fungi. Moreover, data on shifts in traits across environments, important to the development of strategy schemes for macro-organisms, also does not yet exist for fungi. We end by suggesting a way forward to add data. Additional data can open the door to the development of fungi-specific strategy schemes and an associated understanding of the trait and ecological strategy dimensions employed by the world's fungi.

Keywords

Ecological strategy schemes, traits, fungi, plants, animals, nutritional modes, guilds, diversity, imputation, phylogeny.

Introduction

There are ~12 gigatons of fungal carbon in the world, containing ~200 times as much biomass as humans (Bar-On *et al.*, 2018). This biomass is comprised of an unknown number of species, with typical estimates around 2-4 million (Hawksworth & Lücking 2017) but some as high as 165.6 million (Larsen *et al.* 2017). Currently ~144,000 fungal species have been described (https://stateoftheworldsfungi.org/). These species are differentially distributed across the main branches of the fungal phylogeny: the bulk of diversity lies within Ascomycota (~62%) and Basidiomycota (~35%) with remaining diversity (~3%) spread across Mucoromycota, Zoopagomycota, Chytridiomycota, Blastocladiomycota, Cryptomycota and Microsporidia.

While the origins and maintenance of so many species remain a mystery, we are gaining insight into how fungal diversity is distributed around the globe. Historically, it was believed that fungi were not dispersal limited, with any species able to reach any location, discussed in Peay *et al.* (2010) and Adams *et al.* (2013). However, additional sampling has revealed large turnover of fungal taxa across geographical spaces and ecological settings (Green *et al.* 2004; Peay *et al.* 2007, 2010; Talbot *et al.* 2014; Powell *et al.* 2015; Hu *et al.* 2019; Steidinger *et al.* 2019). Additionally, emerging molecular tools, such as high-throughput sequencing (e.g., amplicon and shotgun), are uncovering incredible numbers of individuals, operational taxonomic units (OTUs) and/or species in small spaces (Kembel & Mueller 2014; Tedersoo *et al.* 2014; Taylor *et al.* 2016; Egidi *et al.* 2019; Lee *et al.* 2019). This work complements early observations that a gram of soil can contain 105-106 fungal colony forming units (Waksman 1922) and together these data suggest that we are surrounded by a rich and complex array of fungal taxa.

This diversity raises a number of questions including 1) Why do so many fungal species exist? 2) How can so many species coexist? 3) Are these assemblages assembled via deterministic (Chesson 2000; Chase & Leibold 2003) or neutral (Hubbell 2001) processes? And 4) If deterministic, which processes are most critical? In examining the processes underlying community assembly, it may be that fungal assemblages are random and membership redundant with little predictability as to why a given species is found in that location (Hubbell 2001). Alternatively, deterministic processes could shape the success or failure of each fungal species at each site (Chesson 2000; Chase & Leibold 2003) with deterministic processes leading to assemblages that are predictable based on how species in the metacommunity interact with their environment and each other. As species differ in their ecological strategies (i.e., lifestyles; Table 1), deterministic processes favor some strategies establishing and succeeding in a given environment at a particular time over others. Species presence in a community is thought to be driven by both environmental filtering and biotic interactions winnowing out species unable to persist and compete under those conditions. Most likely, fungal communities fall somewhere on a spectrum between neutral and deterministic assembly (Chave 2004), with parts of their assembly showing strong deterministic processes and a restricted region showing neutral or close to neutral dynamics (Powell *et al.* 2015).

The advent of high-throughput sequencing has rapidly sped up our ability to study fungal communities (Hibbett *et al.* 2009), and, as such, the search for a theoretical framework for fungal community ecology is at a nascent stage (Maherali & Klironomos 2007; Bässler *et al.* 2014; Van Der Wal *et al.* 2016; Phillips *et al.* 2019). Aspects of theory emerging from other taxa may be useful in this effort. Plants, like fungi, are modular and sessile as adults, meaning theories developed in plants may transfer well to fungi, as suggested by Grime (1988) and

Table 1. Strategy schemes developed for various macro-organisms, including their description, potential problems applying them to fungi, original reference(s) and references in which they have been applied to fungi. Note: All schemes present serious problems when applying to fungi. Perhaps the most relevant is the competition-colonization strategy scheme, although only some aspects have yet to be tested in fungi. These issues suggest fungi-specific strategy schemes need to be developed.

Strategy Schemes	Description	Issues applying to fungi	Original references	Fungal references
r - K	Represents tradeoff in reproductive strategies between producing many low investment offspring and few high investment offspring. Assumes parental investment.	Fungi can disperse without reproducing and parental investment does not translate.	McArthur and Wilson E.O., 1967; Pianka, 1970	Andrews and Rouse, 1982; Andrews and Harris, 1986
CSR	Allocates species into competitive, stress tolerators and ruderals.	No directly measurable traits meaning implementation is difficult within and across sites.	Grime, 1974; Weaver and Grime, 1979	Pugh, 1980; Pugh and Boddy, 1988; Boddy and Hiscox, 2016; Chagnon, Rineau and Kaiser, 2016; Maynard *et al.*, 2019
Conservative - acquisitive	Places species along an axis of rates of return on investment with acquisitive species having high rates of acquisition and growth with conservative having the opposite.	Hyphal lifespan is difficult to measure. Specialized short-lifespan tissues are difficult to observe *in situ* or to measure *ex situ*.	Reich *et al.*, 1999	Staddon *et al.*, 2003; Powell and Rillig, 2018
R*	Those with the ability to persist as resources become limiting (i.e., withstand indirect competition) will survive.	Direct competition is common in fungi, resource drawdown may be less important in determining outcomes. Fungi also often inhabit environments where resources are patchy.	Tilman, 1982	Waldrop *et al.* 2006; Werner & Kiers 2015
Competition - colonization	Built on a tradeoff between ability to disperse to versus ability to establish at new sites.	Competitive hierarchies may not be simple	Levins & Culver 1971	Hart *et al.* 2001; Kennedy *et al.* 2011
Body size / metabolic scaling theory	Relates metabolic rates to body size with smaller bodied organisms thought to have higher mass-specific metabolic rates. Scaling slopes established for plants (1) and animals (3/4).	Body size in fungi is difficult both conceptually and practically.	Kleiber, 1947	Aguilar-Trigueros, Rillig and Crowther, 2017
Stoichiometry	Predicts how the ratio of elements behave in organisms and substrates	Plasticity in C:N:P on different substrates makes implementation tricky.	Sterner and Elser, 2002	Johnson, 2010b; Danger, Gessner and Bärlocher, 2016; Zhang and Elser, 2017; Powell and Rillig, 2018
Allometric scaling	Predicts changes in organisms relative to proportional changes in body size.	Body size in fungi is difficult both conceptually and practically.	Corner, 1949	Aguilar-Trigueros, Rillig and Crowther, 2017

Pugh (1980). In other taxa, ecological strategy schemes provide building blocks that shed light on mechanisms potentially allowing coexistence of diverse species assemblages.

An early scheme in plants was developed by Grime (1974) that suggested species could be arrayed along two axes in their environments: degree of stress and degree of disturbance. The expectation was that the axes could be divided into four boxes with species occupying three, described as: 1) competitors = low stress and low disturbance, 2) ruderals = low stress and high disturbance, and 3) stress tolerators = high stress and low disturbance with no species able to tolerate 4) high stress and high disturbance. There is no guidance in this scheme for how to measure a given species' location on these axes and compare these locations among different systems, as tolerating stress or being competitive are emergent properties. This shortcoming was tackled in subsequent schemes in which they directly mapped ecological strategies to the underlying mechanisms via species' functional traits - measurable properties i.e., morphological, anatomical, physiological, behavioral, etc. characteristic of a given species that inform when and where species are observed. We cover the rationale behind this focus below and go into the schemes in further depth in Table 1. In later sections, we highlight schemes we believe are especially ripe for development in understanding fungal community assembly.

The goal for the next generation of functional trait-based ecological strategy schemes (Reich *et al.* 1997, 1999) was to examine the tradeoffs and coordination (strategy axes) among traits that structure co-existence. Traits arise as a consequence of natural selection acting on the phenotype. As organisms must allocate their limited resources to optimize fitness, they cannot devote resources to all traits simultaneously (Bazzaz & Grace 1997). This resource limitation results in coordination in some traits and tradeoffs in others (e.g., for a given mass of leaf tissues leaves can maximize surface area to capture light or maximize thickness to withstand mechanical damage; Weaver & Grime 1979; Southwood 1988; Craine 2009). The trait spaces occupied by different species are constrained by species' available genetic variabilities, competitive abilities and biophysical possibilities (Reich *et al.* 1997; Preston *et al.* 2006). Because of the way these constraints interact with a changing environment in space and time, more than one successful strategy may exist within a particular environment, allowing the co-occurrence of functionally different organisms (Falster *et al.* 2017).

Some of the recognized critical functional traits in macro-organisms are measured at a micro-scale on a given organism (e.g., fine root diameter, vessel length and stomatal density), lending support for the idea of using traits to map fungal strategy schemes. Even so, functional trait data for fungi are only just beginning to emerge and the tool kit is largely limited to a subset of possible traits. Since many fungi are hard to observe, key traits to date focus on non-visual ones, including enzymatic and genetic. For instance, many wood decay fungi have numerous hydrolytic and lignolytic enzymes useful for breaking down complex carbon compounds (Eastwood *et al.* 2011; Riley *et al.* 2014). Other fungi lack various of these enzymes, especially lignolytic, which is strong evidence for an element of determinism in the assembly of wood decaying fungi. However, the dynamics among the species with hydrolytic and lignolytic enzymes may still show aspects of neutral behavior.

The potential for a trait-based ecology of fungi informed by individual strategy schemes developed for macro-organisms has been proposed in or inferred from multiple works (Table 1). This body of trait-based theory may be transferable to fungi, but it requires several major

advances specific to fungi: 1) relevant traits need to be defined from careful study of fungal ecology, not just directly extrapolated from plants or other sessile modular organisms. Many of the existing schemes rely on measures of body size, which are difficult in fungi. Additionally, other key traits for macro-organisms do not occur in fungi (e.g., heterotrophic fungi have no direct analog to leaves in autotrophic plants but do have unique attributes to their fungal hyphae); 2) the distinct nature of fungal ecology e.g., bodies built of networks of hyphae has not been incorporated into strategy schemes for macro-organisms but is necessary for a theory of fungal community assemblies; 3) an approach to assembling and cataloguing the huge diversity of fungal communities needs to be developed. In this review, we discuss progress on all three fronts and describe a research program for moving forward in this final area.

Schemes overview

Many key strategy schemes used for various macro-organisms do not translate well to fungi (Table 1). Below we discuss ways that aspects of the most relevant may apply to, as well as unique challenges presented by, fungi as we strive to understand why so many fungal species exist on earth today. We divide our discussion of these schemes into four categories related to immigration 1) Dispersal and colonization and assembly 2) Growth rates and metabolism, 3) Acquiring and deploying resources, as well as 4) Lifestyle (guild) switching. The first three categories describe how a successful organism begins and lives out its life and the fourth describes a special ability of fungi to switch among lifestyles. As described above, strategies in these categories rest upon the idea that organisms are limited in their resources (Bazzaz & Grace 1997), leading to tradeoffs in strategy and trait space. For instance, parents must choose how to allocate resources across offspring within and across years with consequences for their offsprings' abilities to colonize different sites. Additionally, as organisms grow, they also must choose how to allocate resources to different tissues and functions. These choices lead to variation in morphological and physiological allometries and nutrient distributions both in space and time, including shifting in guild membership. Last, we discuss a major problem applying trait-based theories to fungi: the vast diversity of fungi has never been visually observed and are only known from sequencing; we propose a framework to facilitate data collection and overcome this hurdle.

Fungal Strategy Schemes

1. Dispersal and colonization

Assuming that organisms have finite resources to allocate to reproduction (Smith & Fretwell 1974), offspring size should have a positive effect on individual survival and competitive ability and a negative effect on colonization if larger offspring have limited dispersal (Table 1: Competition-colonization and to a degree r-K). Across plants within habitats, a tradeoff between annual number and size of seeds produced has been observed (Moles & Westoby 2006). On average, taller plants with smaller seeds disperse seeds further (Muller-Landau *et al.* 2008; Thomson *et al.* 2011), while seedlings of larger seeded species have higher survival through early establishment (Moles & Westoby 2006) and are more tolerant of intra- (Lebrija-Trejos *et al.* 2016) and inter-specific neighboring seedlings (Grime & Jeffrey 1965; Walters & Reich 2000) and established vegetation (Westoby *et al.* 2002). Based on these results from plants, a tradeoff is expected between spore number and size across fungal species. It is likely that this tradeoff will be maintained by biophysical constraints (e.g., space is limited in spore sacs, e.g., asci, basidia), as well as selective forces leading to common solutions across fungal taxa, weeding out less competitive strategies. Studies support some of these patterns in fungi.

Spore size and number tradeoff (Chuang & Ko 1983; Aguilar-Trigueros *et al.* 2019), and spore dispersal distance is negatively correlated with spore size (Norros *et al.* 2014). While, to our knowledge, direct evidence of the effect of spore size on the outcome of competitive interactions is lacking, modelling and experimental studies suggest that competitive ability is negatively linked to dispersal ability (Pringle & Taylor 2002; Peay *et al.* 2007; Norros *et al.* 2014; Smith & Brown 2018).

However, using spore size as a proxy for dispersal ability along the colonization-competition strategy axis may be inadequate. The adaptations that fungi possess for maximizing dispersal are diverse in form and function (Ingold 1954). Some fruiting bodies possess structures that serve to propel spores into the air, while spores possess a variety of traits that facilitate their movement via wind, plants, animals and water. In addition, fitness in novel environments appears to have more to do with spore dormancy and longevity than size (Nara 2009). There may be more important traits than large spores enhancing viability in stressful environments, for instance attributes of fungal spore walls. For airborne spores, melanin may serve as protection against ultraviolet radiation over long distances (Jacobson *et al.* 1995), possibly at a cost of slower germination (Halbwachs & Bässler 2015). Incorporating many of these diverse traits into a framework that places species along a fungal ecological strategy axis will be critical.

2. Growth and metabolism

Some existing strategies incorporate how organisms grow (Table 1: to a degree Stoichiometry, Conservative-acquisitive, CSR and Allometric scaling). Growth rate is not itself embedded in these strategies, but rather is a measure of species performance in a particular environment given its ecological strategy. For instance, strategies associated with biological stoichiometry predict that fast growing plants tend to exhibit homeostatic tissue nitrogen:phosphorus (N:P) ratios that are constrained to a narrow range and less tightly linked to supply ratios of N and P in the environment, due to the coupled allocation of these elements into molecules supporting growth RNA molecules and proteins (Sterner & Elser 2002; Elser *et al.* 2010). Work is needed to identify traits in fungi that provide a practical analog for some plant traits along this axis; for example, the N content in hyphae may confound attempts to map fungi on these axes given that it is also a component of structural chitin in addition to a component of molecules associated with growth.

Other elements of schemes focusing on growth may also be useful for fungi. For instance, the energy that fungi absorb can be transferred into metabolism or biomass, with the proportion that leads to biomass often quantified as “carbon use efficiency” (Sinsabaugh *et al.* 2013; Manzoni *et al.* 2018). Within biomass allocation, the energy can be allocated to hyphal growth or storage. Due largely to methodological limitations, carbon use efficiency has typically been measured at the community rather than species level. It is likely that there exists significant heterogeneity among fungal species in both their carbon use efficiency and allocation to growth versus storage, meaning that species level measures of carbon use efficiency for culturable, free-living fungi may prove a tractable trait. However, difficult to culture fungi and particularly those that are usually observed in association with a host will require conceptual and technological innovations. For instance, new approaches are needed to separate the amount of carbon assimilated and respired by a fungus from that associated with other organisms.

Metabolic rates (Table 1: Body size/metabolic scaling theory) have been frequently measured in plants and animals, where it is shown to scale with body size (West *et al.* 1997; Glazier 2008). However, plants and animals typically follow different scaling relations between these variables (animals = ¾ slope, plants = 1 slope), suggesting that metabolism, construction, and transport are governed by different laws between these two groups (Reich *et al.* 2006; Savage *et al.* 2008). In fungi, there have been few attempts to understand the scaling of biological functions with size; this is partly related to the fact that defining fungal body size is challenging (Aguilar-Trigueros *et al.* 2017). Often, we lack anything beyond a sequence for a given fungus, and even when we have fungal tissue in hand, it is hard to differentiate where a given individual begins and ends. One study used colony size to represent body size. They found when marine and ectomycorrhizal fungi were analyzed separately, metabolism scaled with colony size at approximately 0.58 (Aguilar-Trigueros *et al.* 2017), suggesting a lower metabolic rate for body size than recorded in animals and plants.

3. Acquiring and deploying resources

Once organisms establish at a site, they must acquire and deploy resources (Table 1: Stoichiometry and to a degree Conservative-acquisitive, R*, and Allometric scaling). There has been a strong historical focus on plant ecological strategies that drive resource acquisition (Wright *et al.* 2004; Ficken & Wright 2019). However, directly extending this approach to fungi has been problematic because fungi, compared to plants, have very plastic growth characterized by less tissue differentiation; this flexibility allows them to shift along trait and ecological strategy axes in complex ways in response to shifting resources. Capturing key variation in growth strategies has led researchers to describe lists of applicable fungal traits (Table 2), including mycelial architecture, construction investment, and enzyme expression. These traits underpin the diverse fungal nutrient acquisition strategies (Aguilar-Trigueros *et al.* 2015; Treseder & Lennon 2015) that we link to ecological strategy schemes below. We believe these traits provide particularly useful avenues for future studies into fungal ecological strategies and community assembly.

Mycelial architecture, i.e., network structure, plays a significant role in resource acquisition (Van Der Heijden *et al.* 2006; Bebber *et al.* 2007; Aguilar-Trigueros *et al.* 2015; Fricker *et al.* 2017) that is a flexible trait both within and among fungal species (Ritz & Crawford 1990; Kranabetter *et al.* 2009; Olsson *et al.* 2014), potentially allowing co-occurring species to inhabit overlapping spaces but obtain different resources (Lehmann *et al.* 2018). This strategy axis may be key in explaining observable fungal diversity (Koide *et al.* 2007; Van Der Heijden & Scheublin 2007). Mycelial architecture is linked to how resources flow through fungi.

Table 2. Measurable fungal traits. Adapted from Aguilar-Trigueros *et al*. (2015).

Trait category	Measurable traits
Mycelial architecture	Branching frequency, angle, order; Hyphal growth unit length; Internodal length; Lateral dichotomies; Rhizomorph/cord length and width; Runner hyphae length and width; Hyphal exploration type; Fractal dimension
Mycelial construction investment	Oxidases; Lignases; Cellulases; Phosphatases; Chitinases; Proteases; Iron transporters; Aquaporins; Chelators; Siderophores
Metabolism/enzymes	Nutrient concentrations; Stoichiometry (C:N:P); DNA, RNA, polyphosphate and lipid contents; Storage structures; Wall thickness; Hyphal diameter

Fungi can change their network for optimal resource allocation by fusion among genetically similar hyphae to form supracellular networks (Weichert & Fleißner 2015; Fleißner & Serrano 2016). Loops created by these fusions provide physical pathways improving network resilience (Fricker *et al.* 2017). Additionally, mycelia have network recycling (Falconer *et al.* 2005; Heaton *et al.* 2016) in which regions "regress", recycling contents. An open topic of research is predicting cues that direct fungi to strengthen or recycle particular fungal sections (Fricker *et al.* 2017).

Furthermore, fungi use different growth strategies to optimize resource uptake, including hyphae extending slowly and densely (short-range foragers or phalangeal foragers; Boddy 1993, 1999) versus extending rapidly but less-densely (long-range foragers; Agerer 2001). The exploration type influences hyphal coverage per area of soil and functionality of single hyphae. Predictive models are being developed to understand network function. The key is that nutrient availability enables network growth and rapid growth is associated with rapid branching (Fricker *et al.* 2017). In these, network architecture is predicted from morphological characters, e.g., branching frequency and angle, internodal length, fractal dimension, and length and width of hyphal types (Lehmann *et al.* 2018), as well as the quantity and quality of the resources available (Boddy 1999; Boddy *et al.* 2000; Fricker *et al.* 2017), and other biotic factors (Wood *et al.* 2006).

The mycelial construction investment is determined by hyphal structure and, together with external production of enzymes, plays an important role in spatial foraging strategies of fungi. Morphological characters of thin hyphae allow fungi to penetrate deep into substrates and grow through solid material to obtain nutrients (Van der Wal *et al.* 2015). The mycelial construction investment strategy axis includes morphological traits such as wall thickness, hyphal diameter and stoichiometry (Sinsabaugh *et al.* 2008; Aguilar-Trigueros *et al.* 2015). The nutrient content, or stoichiometry, differs among fungal species (Mouginot *et al.* 2014; Tischer *et al.* 2014) and guilds (Zhang & Elser 2017; Kranabetter *et al.* 2019). In all organisms, growth is greatest when neither nitrogen or phosphorus are limiting and both are allocated to compounds required for growth (Elser *et al.* 2003). During growth, N is allocated to structural compounds (e.g., chitin) and proteins and P is allocated to nucleic acids and membrane phospholipids (Bull & Trinci 1977). When nutrient availability exceeds growth requirements, N and P concentrations in vacuoles increase (Kottke *et al.* 1995). In addition to playing a role in translocation of phosphorus to the plant host in mutualistic symbiotic fungi (Bücking & Heyser 1999; Ezawa *et al.* 2004), polyphosphates are associated with conditions of slow growth and stress and their contribution to the total P pool varies among fungal species on the order of 23-65% (Beever & Burns 1981).

Finally, resource acquisition depends on enzyme expression, which functions to increase nutrient availability for uptake (Allison & Vitousek 2005; Aguilar-Trigueros *et al.* 2015; Treseder & Lennon 2015). Because fungi are heterotrophs, they must extract energy from other organisms - living and dead. To do this, most secrete extracellular enzymes to break down compounds obtaining monomers as carbon. Fungi are typically divided into three major nutrient acquisition functional groups: mutualistic, parasitic and saprotrophic (Murphy & Horgan 2005; Nguyen *et al.* 2016; Zeilinger *et al.* 2016). Although these groups differ in the set and expression level of enzymes, genomic studies are showing that a continuous trait-based approach is needed to determine fungal functionality (Peay *et al.* 2016). For example, while mutualistic mycorrhizal and parasitic fungi obtain their carbon via their hosts,

saprotrophs gain their carbon from dead organic materials, such as soil and litter. However, ectomycorrhizal fungi cannot be clearly distinguished from their free-living saprotroph relatives based on enzyme expression alone (Talbot *et al.* 2015). Like their relatives, they can decompose litter and only have lower expression of carbohydrases, acid phosphatases (Talbot *et al.* 2015) and peroxidases (Kyaschenko *et al.* 2017) than their relatives (Rineau *et al.* 2012; Lindahl & Tunlid 2015; Shah *et al.* 2016). Because enzyme expression levels differ dramatically among species, understanding this resource strategy axis is key to understanding fungal functionality, abundance and survival (Šnajdr *et al.* 2011; Eichlerová *et al.* 2015). Depending on the community of fungi, different enzymes are secreted and niches occupied, which has strong ecological effects (Van der Wal *et al.* 2015; Baskaran *et al.* 2017). This axis is likewise an important driver for fungal diversity by driving niche differentiation (Caldwell 2005; Van Der Heijden & Scheublin 2007). In sum, while fungi may acquire resources in different ways to those described already for macro-organisms, a growing body of literature suggests promise in critical fungal traits in resource acquisition and deployment, which should allow for fungal specific strategy schemes.

4. Lifestyle (guild) switching

Fungi present a unique challenge as we attempt to translate ecological strategy schemes from macro-organisms; they traverse ecological guilds and trophic levels (Zanne *et al.* in press; Olson *et al.* 2012; Voriskova & Baldrian 2013; Kuo *et al.* 2014; Martin *et al.* 2015). They are pathogens of animals and plants, causing disease and death in hosts, endophytes existing within host tissues, mutualistic symbionts such as lichens and mycorrhizas exchanging resources with hosts, and saprotrophs decomposing dead organic material (https://github.com/UMNFuN/FUNGuild). Some fungi even exist as parasites on other fungi (i.e., mycoparasites; Barnett 1963). Many fungi can move among being pathogens, mutualists and saprobes over the course of a given individual's life or among individuals of the same species (Zanne *et al.* in press; Olson *et al.* 2012; Voriskova & Baldrian 2013; Kuo *et al.* 2014; Martin *et al.* 2015). It may be that the ecological strategies and the traits that underpin those strategies change with a change in guild, requiring different schemes applied within and across species.

Plants also show a range of guilds from carnivore to parasite to epiphyte, but this range has largely been ignored by both trait ecology and coexistence models, under the assumption that most "important" plants share the same, free-standing, autotrophic strategy. This type of assumption is less defensible in fungi, as there are more species that switch guilds, and it is expected that switching offers a competitive edge. For example, saprotrophs often already occupy wood as endophytes and have a distinct advantage in competing for resources as compared to species that need to disperse to the substrate (Parfitt *et al.* 2010). Similarly, the dynamics of switching between mutualist and saprobe is an important part of the ecology of many mycorrhizal fungi (Talbot *et al.* 2008, but see Lindahl and Tunlid 2015). As strategy schemes are developed for fungi, they must incorporate the incredible ability of fungi to readily move among guilds as it is clearly the rule, not the exception.

Research Program: Towards an understanding of fungal traits and strategy schemes across gradients

Our review of existing ecological strategy axes developed for macro-organisms, suggests that many of them will not be readily recycled to fungi. For instance, many rely upon visual observations of organisms, especially measures of body size, which are not feasible for many fungi. These findings suggest that while elements of existing schemes may be useful,

new ones must be developed. Empirical data were key to the development of functional strategy schemes for various macro-organisms. For example, shifts in plant trait distributions across different soil types and grazing pressures near Sheffield were two of a number of key empirical observations that lead to the CSR scheme (Grime 1974). One critical empirical limitation in the development of fungal strategy schemes is the lack of data to make analogous observations.

Fungal diversity at all scales is daunting. Even more troublesome is that, unlike for various macro-organisms, it is often impossible to isolate an individual species to measure traits. This challenge creates a difficult problem for fungal ecologists: they can use high-throughput sequencing to measure amplicon or shotgun sequences for operational taxonomic units ("species") in a community, but are able to isolate only a small subset of these organisms for further study. The traits and strategies of the unisolated species remain a mystery. This limitation prevents key observations such as those that lead to CSR and other strategy schemes.

Central to this process is the need to fill gaps in the available trait data (Zanne *et al.* in press), particularly with fungal species that are difficult to culture or are only found in association with hosts. Linking high-throughput sequences to traits and strategies will open an array of research opportunities in fungal ecology and evolutionary biology, leading to a new golden age for fungal function. For an example of how this might be done, we consider growth, which relates to many ecological strategy schemes (Table 1) but is challenging to measure for species of fungi that cannot be observed *in-vitro* since it is difficult to assess their biomass or surface area. Combining measures of these traits on environmental samples with DNA-based tools to identify species may be an indirect way to characterize their growth. Investigations into fungal growth going back to Tomkins (1932), focusing on hyphal extension and branching, suggest ways to extrapolate to growth from a portion of a mycelium. The frequency of hyphal tip production can be inferred from the length between branches (Trinci 1974). Steele & Trinci (1975) observed that hyphal extension was strongly correlated with the length of the extension zone, from the tip of the extending hypha where hyphal diameter is expanding to its base where the wall has matured and hyphal diameter is fixed. These measures can be made so that samples are left intact to then use DNA sequencing to identify species present.

Furthermore, much may be gleaned from the combined use of trait data measured on species and high-throughput amplicon or shotgun sequencing of environmental samples to map the distribution of fungal species and their traits across environments and infer the deterministic drivers of fungal community assembly. However, for many traits, the tools and resources are not yet available. Below we outline the steps necessary for this to occur:

1. Measuring more species for a narrow set of traits (Aguilar-Trigueros *et al.* 2015) in standard conditions. In plants, growth experiments have assembled large databases of relative growth rates, in a process originally called "trait screening" (Grime *et al.* 1997; Poorter *et al.* 2019). The process of assembling fungal data has begun (Zanne *et al.* in press; Aguilar-Trigueros *et al.* 2015; Treseder & Lennon 2015; Dawson *et al.* 2019); https://github.com/traitecoevo/fungaltraits), but we need to assemble larger, more-comprehensive, global databases starting with an agreed upon set of traits relevant to important ecological strategies (e.g., Table 2).
2. Linking trait measures to sequence data collected from voucher specimens and other

sampled fungi via repeatable pipelines using taxonomic names and/or accession numbers. These links will allow us to apply trait values to species we find in different communities.
3. Building a comprehensive phylogeny of fungi populated by taxa with trait values.
4. Modelling evolution of traits on the phylogeny, including understanding the tempo and mode, sensu Simpson (1944), of trait evolution (e.g., test for adequacy of different evolutionary models). Building a phylogeny and modelling trait evolution will let us determine the importance of evolutionary history in shaping community assembly, and understand how different traits evolved across the fungal tree of life.
5. Using modern mapping and grafting methods to add novel amplicon sequences lacking trait values to the phylogeny (Beaulieu *et al.* 2012; Smith *et al.* 2013; Smith & Brown 2018). As we have only uncovered a small slice of fungal diversity, it will be critical to grow our evolutionary tree as we discover more of this hidden diversity.
6. Computing trait values for the amplicon sequences along with associated uncertainty (due to phylogenetic, trait, and imputation uncertainty). Methods for this already exist (Fitzjohn *et al.* 2014; Penone *et al.* 2014; Swenson 2014; Schrodt *et al.* 2015) and the choice of specific methods will be informed by the results of (4). As taxa missing trait values are added to the phylogeny, we can predict what trait and ecological strategy space they may occupy. These estimates may in some cases be directly used in analyses of communities and in others provide testable hypotheses as we are able to collect trait data directly for those species.

These steps have been useful in shaping our understanding of, for instance, plant functional ecology, evolution and community assembly. They should similarly facilitate rapid growth in our understanding of fungi and be attainable in the next 10 years of fungal research. As linked databases and tools are created, novel answers to outstanding questions will be found, as well as insight into a new generation of strategy schemes specific for fungi. We believe we can open the door to previously unanswerable questions about fungal functional ecology including: How redundant are fungal communities? Does the growth rate of fungi slow as succession proceeds in forests? Do fungi in patchier soils show different hyphal branching networks than homogenous soils? Is fungal community assembly dominated by habitat filtering or is there also a role for limiting similarity? Is the average growth rate of tropical fungi faster than temperate fungi? Do urban fungi have different traits than those from natural habitats? Are climate change and intensification of land use exerting selection on traits associated with growth and resource allocation? Do the traits of mycorrhizal symbionts change as a tree matures? Are fungi able to change ecological strategies and traits as they shift their nutritional modes, as their host substrate changes, and/or as they interact with other fungi in their community? These questions are interesting in their own right, but also the answers will provide the key empirical data to develop fungi-specific strategy schemes.

Conclusion

We propose that recycling ecological strategy schemes developed for macro-organisms is a worthwhile starting point for developing a functional understanding of fungal diversity; however, translating many of these existing schemes will prove challenging. We have provided an overview of hurdles associated with fungi that need to be overcome, including elements of their biologies and life histories that are special and suggest that existing ecological strategies may need to be rethought or revised. For instance, many existing ecological strategy schemes rely on measures of body size, which is often difficult to define

for fungi. Particularly challenging is filling the massive gap in data required to map the diversity of fungi to ecological strategy schemes, but the research program we have proposed has tremendous potential to make a substantial contribution toward this effort. Realizing this potential will require the combined efforts of mycologists and those from many other disciplines (physiology, molecular biology, ecological informatics, phylogenomics, etc.).

Acknowledgements

We thank the reviewers of our original manuscript for providing useful comments. Support for this work came from the National Science Foundation (DEB: 1623040, "MacroMycoFunc - Forming an integrated understanding of function across fungi" and DEB: 1655759; "Collaborative Research: NSFDEB-NERC: Tropical deadwood carbon fluxes: Improving carbon models by incorporating termites and microbes" to AEZ), Australian Research Council Discovery Grant (DP160103765: "Closing the carbon cycle: an ecological understanding of wood decay" to WKC, JRP, and AEZ), and European Research Council (ERC 335542 to ETK).

Author contributions

AZ, JP, HFM, ETK, AP and WKC were all involved in writing and revision of the document.

References

Adams, R.I., Miletto, M., Taylor, J.W. & Bruns, T.D. (2013). Dispersal in microbes: Fungi in indoor air are dominated by outdoor air and show dispersal limitation at short distances. *ISME Journal*, 7, 1262–1273, doi: 10.1038/ismej.2013.28.

Agerer, R. (2001). Exploration types of ectomycorrhizae: A proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. *Mycorrhiza*, 11, 107–114, doi: 10.1007/s005720100108.

Aguilar-Trigueros, C.A., Hempel, S., Powell, J.R., Anderson, I.C., Antonovics, J., Bergmann, J., *et al.* (2015). Branching out: Towards a trait-based understanding of fungal ecology. *Fungal Biology Reviews*, 29, 34–41, doi: 10.1016/j.fbr.2015.03.001.

Aguilar-Trigueros, C.A., Hempel, S., Powell, J.R., Cornwell, W.K. & Rillig, M.C. (2019). Bridging reproductive and microbial ecology: a case study in arbuscular mycorrhizal fungi. *ISME Journal*, 13, 873–884, doi: 10.1038/s41396-018-0314-7.

Aguilar-Trigueros, C.A., Rillig, M.C. & Crowther, T.W. (2017). Applying allometric theory to fungi. *ISME Journal*, 11, 2175–2180, doi: 10.1038/ismej.2017.86.

Allison, S.D. & Vitousek, P.M. (2005). Responses of extracellular enzymes to simple and complex nutrient inputs. *Soil Biology and Biochemistry*, 37, 937–944, doi: 10.1016/j.soilbio.2004.09.014.

Barnett, H.L. (1963). The Nature of Mycoparasitism by Fungi. *Annual Review of Microbiology*, 17, 1–14, doi: 10.1146/annurev.mi.17.100163.000245.

Baskaran, P., Hyvönen, R., Berglund, S.L., Clemmensen, K.E., Ågren, G.I., Lindahl, B.D., *et al.* (2017). Modelling the influence of ectomycorrhizal decomposition on plant nutrition and soil carbon sequestration in boreal forest ecosystems. *New Phytologist*, 213, 1452–1465, doi: 10.1111/nph.14213.

Bässler, C., Ernst, R., Cadotte, M., Heibl, C. & Müller, J. (2014). Near-to-nature logging influences fungal community assembly processes in a temperate forest. *Journal of Applied Ecology*, doi: 10.1111/1365-2664.12267.

Bazzaz, F. & Grace, J. (Eds.). (1997). *Plant Resource Allocation*. Elsevier.

Beaulieu, J.M., Ree, R.H., Cavender-Bares, J., Weiblen, G.D. & Donoghue, M.J. (2012). Synthesizing phylogenetic knowledge for ecological research. *Ecology*, 93, S4–S13, doi: 10.1890/11-0638.1.

Bebber, D.P., Hynes, J., Darrah, P.R., Boddy, L. & Fricker, M.D. (2007). Biological solutions to transport network design. *Proceedings of the Royal Society B: Biological Sciences*, 274, 2307–2315, doi: 10.1098/rspb.2007.0459.

Beever, R.E. & Burns, D.J.W. (1981). Phosphorus Uptake, Storage and Utilization by Fungi. *Advances in Botanical Research*, 8, 127–219, doi: 10.1016/S0065-2296(08)60034-8.

Boddy, L. (1993). Saprotrophic cord-forming fungi: warfare strategies and other ecological aspects. *Mycological Research*, 97, 641–655, doi: 10.1016/S0953-7562(09)80141-X.

Boddy, L. (1999). Saprotrophic cord-forming fungi: meeting the challenge of heterogeneous environments. *Mycologia*, 91, 13–32, doi: 10.1080/00275514.1999.12060990.

Boddy, L., Wells, J.M., Culshaw, C. & Donnelly, D.P. (2000). Fractal analysis in studies of mycelium in soil. *Developments in Soil Science*, 27, 211–238, doi: 10.1016/S0166-2481(00)80014-8.

Bücking, H. & Heyser, W. (1999). Elemental composition and function of polyphosphates in ectomycorrhizal fungi - An X-ray microanalytical study. *Mycological Research*, 103, 31–39, doi: 10.1017/S0953756298006935.
Bull, A.T. & Trinci, A.P.J. (1977). The Physiology and Metabolic Control of Fungal Growth. *Advances in Microbial Physiology*, 15, 1–84, doi: 10.1016/S0065-2911(08)60314-8.
Caldwell, B.A. (2005). Enzyme activities as a component of soil biodiversity: A review. *Pedobiologia*, 49, 637–644, doi: 10.1016/j.pedobi.2005.06.003.
Chase, J. & Leibold, M. (2003). *Ecological Niches*. The University of Chicago Press, Chicago, IL, USA.
Chave, J. (2004). Neutral theory and community ecology. *Ecology Letters*, 7, 241–253, doi: 10.1111/j.1461-0248.2003.00566.x.
Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics*, 31, 343–366, doi: 10.1146/annurev.ecolsys.31.1.343.
Chuang, T.Y.Y. & Ko, W.H.H. (1983). Propagule size: Its relation to longevity and reproductive capacity. *Soil Biology and Biochemistry*, 15, 269–274, doi: 10.1016/0038-0717(83)90070-6.
Craine, J.M. (2009). *Resource strategies of wild plants*. *Resource Strategies of Wild Plants*. Princeton University Press, New Jersey.
Dawson, S.K., Boddy, L., Halbwachs, H., Bässler, C., Andrew, C., Crowther, T.W., *et al.* (2019). Handbook for the measurement of macrofungal functional traits: A start with basidiomycete wood fungi. *Functional Ecology*, 33, 372–387, doi: 10.1111/1365-2435.13239.
Eastwood, D.C., Floudas, D., Binder, M., Majcherczyk, A., Schneider, P., Aerts, A., *et al.* (2011). The Plant Cell Wall-Decomposing Machinery Underlies the Functional Diversity of Forest Fungi. *Science*, 333, 762–765, doi: 10.1126/science.1205411.
Egidi, E., Delgado-Baquerizo, M., Plett, J.M., Wang, J., Eldridge, D.J., Bardgett, R.D., *et al.* (2019). A few Ascomycota taxa dominate soil fungal communities worldwide. *Nature Communications*, 10, 2369, doi: 10.1038/s41467-019-10373-z.
Eichlerová, I., Homolka, L., Žifčáková, L., Lisá, L., Dobiášová, P. & Baldrian, P. (2015). Enzymatic systems involved in decomposition reflects the ecology and taxonomy of saprotrophic fungi. *Fungal Ecology*, 13, 10–22, doi: 10.1016/j.funeco.2014.08.002.
Elser, J.J., Acharya, K., Kyle, M., Cotner, J., Makino, W., Markow, T., *et al.* (2003). Growth rate-stoichiometry couplings in diverse biota. *Ecology Letters*, 6, 936–943, doi: 10.1046/j.1461-0248.2003.00518.x.
Elser, J.J., Fagan, W.F., Kerkhoff, A.J., Swenson, N.G. & Enquist, B.J. (2010). Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. *New Phytologist*, 186, 593–608, doi: 10.1111/j.1469-8137.2010.03214.x.
Ezawa, T., Cavagnaro, T.R., Smith, S.E., Smith, F.A. & Ohtomo, R. (2004). Rapid accumulation of polyphosphate in extraradical hyphae of an arbuscular mycorrhizal fungus as revealed by histochemistry and a polyphosphate kinase/luciferase system. *New Phytologist*, 161, 387–392, doi: 10.1046/j.1469-8137.2003.00966.x.
Falconer, R.E., Bown, J.L., White, N.A. & Crawford, J.W. (2005). Biomass recycling and the origin of phenotype in fungal mycelia. *Proceedings of the Royal Society B: Biological Sciences*, 272, 1727–1734, doi: 10.1098/rspb.2005.3150.
Falster, D.S., Brännström, Å., Westoby, M. & Dieckmann, U. (2017). Multitrait successional forest dynamics enable diverse competitive coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, 114, E2719–E2728, doi: 10.1073/pnas.1610206114.
Ficken, C.D. & Wright, J.P. (2019). Nitrogen uptake and biomass resprouting show contrasting relationships with resource acquisitive and conservative plant traits. *Journal of Vegetation Science*, 30, 65–74, doi: 10.1111/jvs.12705.
Fitzjohn, R.G., Pennell, M.W., Zanne, A.E., Stevens, P.F., Tank, D.C. & Cornwell, W.K. (2014). How much of the world is woody? *Journal of Ecology*, 102, 1266–1272, doi: 10.1111/1365-2745.12260.
Fleißner, A. & Serrano, A. (2016). 7 The Art of Networking: Vegetative Hyphal Fusion in Filamentous Ascomycete Fungi. *Growth, Differentiation and Sexuality*, 133–153, doi: 10.1007/978-3-319-25844-7_7.
Fricker, M.D., Heaton, L.L.M., Jones, N.S. & Boddy, L. (2017). The Mycelium as a Network. In: *The Fungal Kingdom*. American Society of Microbiology, pp. 335–367.
Glazier, D.S. (2008). Effects of metabolic level on the body size scaling of metabolic rate in birds and mammals. *Proceedings of the Royal Society B: Biological Sciences*, 275, 1405–1410, doi: 10.1098/rspb.2008.0118.
Green, J.L., Holmes, A.J., Westoby, M., Oliver, I., Briscoe, D., Dangerfield, M., *et al.* (2004). Spatial scaling of microbial diversity. *Nature*, 432, 747–750, doi: 10.1038/nature03034.
Grime, J.P. (1974). Vegetation classification by reference to strategies. *Nature*, 250, 26–31, doi: 10.1038/250026a0.
Grime, J.P. (1988). Fungal strategies in ecological perspective. *Proceedings of the Royal Society of Edinburgh. Section B. Biological Sciences*, 94, 167–169, doi: 10.1017/s0269727000007260.
Grime, J.P. & Jeffrey, D.W. (1965). Seedling Establishment in Vertical Gradients of Sunlight. *The Journal of Ecology*, 53, 621, doi: 10.2307/2257624.
Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., *et al.* (1997). Integrated Screening Validates Primary Axes of Specialisation in Plants. *Oikos*, 79, 259, doi: 10.2307/3546011.
Halbwachs, H. & Bässler, C. (2015). Gone with the wind - A review on basidiospores of lamellate agarics. *Mycosphere*, doi: 10.5943/mycosphere/6/1/10.
Hawksworth, D.L.D. & Lücking, R. (2017). Fungal Diversity Revisited: 2.2 to 3.8 Million Species. In: *The Fungal Kingdom*. American Society of Microbiology, pp. 79–95.
Heaton, L.L.M.M., Jones, N.S. & Fricker, M.D. (2015). Energetic Constraints on Fungal Growth. *The American*

Naturalist, 187, E27–E40, doi: 10.1086/684392.
Van Der Heijden, M.G.A.A. & Scheublin, T.R. (2007). Functional traits in mycorrhizal ecology: their use for predicting the impact of arbuscular mycorrhizal fungal communities on plant growth and ecosystem functioning. *New Phytologist*, 174, 244–250, doi: 10.1111/j.1469-8137.2007.02041.x.
Van Der Heijden, M.G.A.A., Streitwolf-Engel, R., Riedl, R., Siegrist, S., Neudecker, A., Ineichen, K., *et al.* (2006). The mycorrhizal contribution to plant productivity, plant nutrition and soil structure in experimental grassland. *New Phytologist*, 172, 739–752, doi: 10.1111/j.1469-8137.2006.01862.x.
Hibbett, D.S., Ohman, A. & Kirk, P.M. (2009). Fungal ecology catches fire. *New Phytologist*, 184, 279–282, doi: 10.1111/j.1469-8137.2009.03042.x.
Hu, Y., Veresoglou, S.D., Tedersoo, L., Xu, T., Ge, T., Liu, L., *et al.* (2019). Contrasting latitudinal diversity and co-occurrence patterns of soil fungi and plants in forest ecosystems. *Soil Biology and Biochemistry*, 131, 100–110, doi: 10.1016/j.soilbio.2019.01.001.
Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*. Princeton University Press.
Ingold, C.T. (1954). *Dispersal in Fungi*. Clarendon Press, Oxford.
Jacobson, E.S., Hove, E. & Emery, H.S. (1995). Antioxidant function of melanin in black fungi. *Infection and Immunity*, 63, 4944–4945.
Kembel, S.W. & Mueller, R.C. (2014). Plant traits and taxonomy drive host associations in tropical Phyllosphere fungal communities1. *Botany*, 92, 303–311, doi: 10.1139/cjb-2013-0194.
Koide, R.T., Courty, P.-E.E. & Garbaye, J. (2007). Research perspectives on functional diversity in ectomycorrhizal fungi. *New Phytologist*, 174, 240–243, doi: 10.1111/j.1469-8137.2007.01987.x.
Kottke, I., Holopainen, T., Alanen, E. & Turnau, K. (1995). Deposition of nitrogen in vacuolar bodies of Cenococcum geophilum Fr. mycorrhizas as detected by electron energy loss spectroscopy. *New Phytologist*, 129, 411–416, doi: 10.1111/j.1469-8137.1995.tb04311.x.
Kranabetter, J.M., Durall, D.M. & MacKenzie, W.H. (2009). Diversity and species distribution of ectomycorrhizal fungi along productivity gradients of a southern boreal forest. *Mycorrhiza*, 19, 99–111, doi: 10.1007/s00572-008-0208-z.
Kranabetter, J.M., Harman-Denhoed, R. & Hawkins, B.J. (2019). Saprotrophic and ectomycorrhizal fungal sporocarp stoichiometry (C : N : P) across temperate rainforests as evidence of shared nutrient constraints among symbionts. *New Phytologist*, 221, 482–492, doi: 10.1111/nph.15380.
Kuo, H.C., Hui, S., Choi, J., Asiegbu, F.O., Valkonen, J.P.T. & Lee, Y.H. (2014). Secret lifestyles of Neurospora crassa. *Scientific Reports*, 4, doi: 10.1038/srep05135.
Kyaschenko, J., Clemmensen, K.E., Karltun, E. & Lindahl, B.D. (2017). Below-ground organic matter accumulation along a boreal forest fertility gradient relates to guild interaction within fungal communities. *Ecology Letters*, 20, 1546–1555, doi: 10.1111/ele.12862.
Larsen, B.B., Miller, E.C., Rhodes, M.K. & Wiens, J.J. (2017). Inordinate Fondness Multiplied and Redistributed: the Number of Species on Earth and the New Pie of Life. *The Quarterly Review of Biology*, 92, 229–265, doi: 10.1086/693564.
Lebrija-Trejos, E., Reich, P.B., Hernández, A. & Wright, S.J. (2016). Species with greater seed mass are more tolerant of conspecific neighbours: a key driver of early survival and future abundances in a tropical forest. *Ecology Letters*, 19, 1071–1080, doi: 10.1111/ele.12643.
Lee, M.R., Powell, J.R., Oberle, B., Cornwell, W.K., Lyons, M., Rigg, J.L., *et al.* (2019). Good neighbors aplenty: fungal endophytes rarely exhibit competitive exclusion patterns across a span of woody habitats. *Ecology*, doi: 10.1002/ecy.2790.
Lehmann, A., Zheng, W., Soutschek, K. & Rillig, M.C. (2018). How to build a mycelium: tradeoffs in fungal architectural traits. *bioRxiv*, 361253, doi: 10.1101/361253.
Lindahl, B.D. & Tunlid, A. (2015). Ectomycorrhizal fungi - potential organic matter decomposers, yet not saprotrophs. *New Phytologist*, 205, 1443–1447, doi: 10.1111/nph.13201.
Maherali, H. & Klironomos, J.N. (2007). Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science*, doi: 10.1126/science.1143082.
Manzoni, S., Čapek, P., Porada, P., Thurner, M., Winterdahl, M., Beer, C., *et al.* (2018). Reviews and syntheses: Carbon use efficiency from organisms to ecosystems - Definitions, theories, and empirical evidence. *Biogeosciences*, 15, 5929–5949, doi: 10.5194/bg-15-5929-2018.
Martin, R., Gazis, R., Skaltsas, D., Chaverri, P. & Hibbett, D. (2015). Unexpected diversity of basidiomycetous endophytes in sapwood and leaves of Hevea. *Mycologia*, 107, 284–297, doi: 10.3852/14-206.
Moles, A.T. & Westoby, M. (2006). Seed size and plant strategy across the whole life cycle. *Oikos*, 113, 91–105, doi: 10.1111/j.0030-1299.2006.14194.x.
Mouginot, C., Kawamura, R., Matulich, K.L., Berlemont, R., Allison, S.D., Amend, A.S., *et al.* (2014). Elemental stoichiometry of Fungi and Bacteria strains from grassland leaf litter. *Soil Biology and Biochemistry*, 76, 278–285, doi: 10.1016/j.soilbio.2014.05.011.
Muller-Landau, H.C., Wright, S.J., Calderón, O., Condit, R. & Hubbell, S.P. (2008). Interspecific variation in primary seed dispersal in a tropical forest. *Journal of Ecology*, 96, 653–667, doi: 10.1111/j.1365-2745.2008.01399.x.
Murphy, R.A. & Horgan, K.A. (2005). Antibiotics, Enzymes and Chemical Commodities from Fungi. In: *Fungi*. John Wiley & Sons, Ltd, Chichester, UK, pp. 113–143.
Nara, K. (2009). Spores of ectomycorrhizal fungi: ecological strategies for germination and dormancy. *New Phytol-*

ogist, 181, 245–248, doi: 10.1111/j.1469-8137.2008.02691.x.
Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., *et al.* (2016). FUNGuild : An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology*, 20, 241–248, doi: 10.1016/j.funeco.2015.06.006.
Norros, V., Rannik, Ü., Hussein, T., Petäjä, T., Vesala, T. & Ovaskainen, O. (2014). Do small spores disperse further than large spores? *Ecology*, 95, 1612–1621, doi: 10.1890/13-0877.1.
Olson, Å., Aerts, A., Asiegbu, F., Belbahri, L., Bouzid, O., Broberg, A., *et al.* (2012). Insight into trade-off between wood decay and parasitism from the genome of a fungal forest pathogen. *New Phytologist*, 194, 1001–1013, doi: 10.1111/j.1469-8137.2012.04128.x.
Olsson, O., Olsson, P.A. & Hammer, E.C. (2014). Phosphorus and carbon availability regulate structural composition and complexity of AM fungal mycelium. *Mycorrhiza*, 24, 443–451, doi: 10.1007/s00572-014-0557-8.
Parfitt, D., Hunt, J., Dockrell, D., Rogers, H.J. & Boddy, L. (2010). Do all trees carry the seeds of their own destruction? PCR reveals numerous wood decay fungi latently present in sapwood of a wide range of angiosperm trees. *Fungal Ecology*, 3, 338–346, doi: 10.1016/j.funeco.2010.02.001.
Peay, K.G., Bidartondo, M.I. & Elizabeth Arnold, A. (2010). Not every fungus is everywhere: scaling to the biogeography of fungal-plant interactions across roots, shoots and ecosystems. *New Phytologist*, 185, 878–882, doi: 10.1111/j.1469-8137.2009.03158.x.
Peay, K.G., Bruns, T.D., Kennedy, P.G., Bergemann, S.E. & Garbelotto, M. (2007). A strong species-area relationship for eukaryotic soil microbes: Island size matters for ectomycorrhizal fungi. *Ecology Letters*, 10, 470–480, doi: 10.1111/j.1461-0248.2007.01035.x.
Peay, K.G., Kennedy, P.G. & Talbot, J.M. (2016). Dimensions of biodiversity in the Earth mycobiome. *Nature Reviews Microbiology*, 14, 434–447, doi: 10.1038/nrmicro.2016.59.
Penone, C., Davidson, A.D., Shoemaker, K.T., Di Marco, M., Rondinini, C., Brooks, T.M., *et al.* (2014). Imputation of missing data in life-history trait datasets: Which approach performs the best? *Methods in Ecology and Evolution*, 5, 1–10, doi: 10.1111/2041-210X.12232.
Phillips, M.L., Weber, S.E., Andrews, L. V., Aronson, E.L., Allen, M.F. & Allen, E.B. (2019). Fungal community assembly in soils and roots under plant invasion and nitrogen deposition. *Fungal Ecology*, doi: 10.1016/j.funeco.2019.01.002.
Poorter, H., Niinemets, Ü., Ntagkas, N., Siebenkäs, A., Mäenpää, M., Matsubara, S., *et al.* (2019). A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. *New Phytologist*, 223, 1073–1105, doi: 10.1111/nph.15754.
Powell, J.R., Karunaratne, S., Campbell, C.D., Yao, H., Robinson, L. & Singh, B.K. (2015). Deterministic processes vary during community assembly for ecologically dissimilar taxa. *Nature Communications*, 6, 8444, doi: 10.1038/ncomms9444.
Preston, K.A., Cornwell, W.K. & DeNoyer, J.L. (2006). Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytologist*, 170, 807–818, doi: 10.1111/j.1469-8137.2006.01712.x.
Pringle, A. & Taylor, J.W. (2002). The fitness of filamentous fungi. *Trends in Microbiology*, 10, 474–481, doi: 10.1016/S0966-842X(02)02447-2.
Pugh, G.J.F. (1980). Strategies in fungal ecology. *Transactions of the British Mycological Society*, 75, IN1-14, doi: 10.1016/s0007-1536(80)80188-4.
Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C., *et al.* (1999). Generality of leaf trait relationships: A test across six biomes. *Ecology*, 80, 1955–1969, doi: 10.1890/0012-9658(1999)080[1955:GOLTRA]2.0.CO;2.
Reich, P.B., Tjoelker, M.G., Machado, J.L. & Oleksyn, J. (2006). Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature*, 439, 457–461, doi: 10.1038/nature04282.
Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 13730–13734, doi: 10.1073/pnas.94.25.13730.
Riley, R., Grigoriev, I. V., Hibbett, D.S., Otillar, R., Lindquist, E.A., Baker, S.E., *et al.* (2014). Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. *Proceedings of the National Academy of Sciences*, 111, 9923–9928, doi: 10.1073/pnas.1400592111.
Rineau, F., Roth, D., Shah, F., Smits, M., Johansson, T., Canbäck, B., *et al.* (2012). The ectomycorrhizal fungus Paxillus involutus converts organic matter in plant litter using a trimmed brown-rot mechanism involving Fenton chemistry. *Environmental Microbiology*, 14, 1477–1487, doi: 10.1111/j.1462-2920.2012.02736.x.
Ritz, K. & Crawford, J. (1990). Quantification of the fractal nature of colonies of Trichoderma viride. *Mycological Research*, 94, 1138–1141, doi: 10.1016/S0953-7562(09)81346-4.
Savage, V.M., Deeds, E.J. & Fontana, W. (2008). Sizing Up Allometric Scaling Theory. *PLoS Computational Biology*, 4, e1000171, doi: 10.1371/journal.pcbi.1000171.
Schrodt, F., Kattge, J., Shan, H., Fazayeli, F., Joswig, J., Banerjee, A., *et al.* (2015). BHPMF - a hierarchical Bayesian approach to gap-filling and trait prediction for macroecology and functional biogeography. *Global Ecology and Biogeography*, 24, 1510–1521, doi: 10.1111/geb.12335.
Shah, F., Nicolás, C., Bentzer, J., Ellström, M., Smits, M., Rineau, F., *et al.* (2016). Ectomycorrhizal fungi decompose soil organic matter using oxidative mechanisms adapted from saprotrophic ancestors. *New Phytologist*, 209, 1705–1719, doi: 10.1111/nph.13722.
Simpson, G.G. (1944). Tempo and mode in evolution. *Transactions of the New York Academy of Sciences*, 8, 45–60.

Sinsabaugh, R.L., Lauber, C.L., Weintraub, M.N., Ahmed, B., Allison, S.D., Crenshaw, C., *et al.* (2008). Stoichiometry of soil enzyme activity at global scale. *Ecology Letters*, 11, 1252–1264, doi: 10.1111/j.1461-0248.2008.01245.x.

Sinsabaugh, R.L., Manzoni, S., Moorhead, D.L. & Richter, A. (2013). Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling. *Ecology Letters*, 16, 930–939, doi: 10.1111/ele.12113.

Smith, C.C. & Fretwell, S.D. (1974). The Optimal Balance between Size and Number of Offspring. *The American Naturalist*, 108, 499–506, doi: 10.1086/282929.

Smith, S.A. & Brown, J.W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105, 302–314, doi: 10.1002/ajb2.1019.

Smith, S.A., Brown, J.W. & Hinchliff, C.E. (2013). Analyzing and Synthesizing Phylogenies Using Tree Alignment Graphs. *PLoS Computational Biology*, 9, e1003223, doi: 10.1371/journal.pcbi.1003223.

Šnajdr, J., Dobiášová, P., Větrovský, T., Valášková, V., Alawi, A., Boddy, L., *et al.* (2011). Saprotrophic basidiomycete mycelia and their interspecific interactions affect the spatial distribution of extracellular enzymes in soil. *FEMS Microbiology Ecology*, 78, 80–90, doi: 10.1111/j.1574-6941.2011.01123.x.

Southwood, T.R.E. (1988). Tactics, Strategies and Templets. *Oikos*, 52, 3, doi: 10.2307/3565974.

Steele, G.C. & Trinci, A.P.J. (1975). the Extension Zone of Mycelial Hyphae. *New Phytologist*, 75, 583–587, doi: 10.1111/j.1469-8137.1975.tb01424.x.

Steidinger, B.S., Crowther, T.W., Liang, J., Van Nuland, M.E., Werner, G.D.A., Reich, P.B., *et al.* (2019). Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature*, 569, 404–408, doi: 10.1038/s41586-019-1128-0.

Sterner, R.. & Elser, J.. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, New Jersey.

Swenson, N.G. (2014). Phylogenetic imputation of plant functional trait databases. *Ecography*, 37, 105–110, doi: 10.1111/j.1600-0587.2013.00528.x.

Talbot, J.M., Allison, S.D. & Treseder, K.K. (2008). Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. *Functional Ecology*, 22, 955–963, doi: 10.1111/j.1365-2435.2008.01402.x.

Talbot, J.M., Bruns, T.D., Taylor, J.W., Smith, D.P., Branco, S., Glassman, S.I., *et al.* (2014). Endemism and functional convergence across the North American soil mycobiome. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 6341–6346, doi: 10.1073/pnas.1402584111.

Talbot, J.M., Martin, F., Kohler, A., Henrissat, B. & Peay, K.G. (2015). Functional guild classification predicts the enzymatic role of fungi in litter and soil biogeochemistry. *Soil Biology and Biochemistry*, 88, 441–456, doi: 10.1016/j.soilbio.2015.05.006.

Taylor, D.L., Walters, W.A., Lennon, N.J., Bochicchio, J., Krohn, A., Caporaso, J.G., *et al.* (2016). Accurate estimation of fungal diversity and abundance through improved lineage-specific primers optimized for Illumina amplicon sequencing. *Applied and Environmental Microbiology*, 82, 7217–7226, doi: 10.1128/AEM.02576-16.

Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., *et al.* (2014). Global diversity and geography of soil fungi. *Science*, 346, doi: 10.1126/science.1256688.

Thomson, F.J., Moles, A.T., Auld, T.D. & Kingsford, R.T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, 99, 1299–1307, doi: 10.1111/j.1365-2745.2011.01867.x.

Tischer, A., Potthast, K. & Hamer, U. (2014). Land-use and soil depth affect resource and microbial stoichiometry in a tropical mountain rainforest region of southern Ecuador. *Oecologia*, 175, 375–393, doi: 10.1007/s00442-014-2894-x.

Tomkins, R.G. (1932). Measuring growth: The Petridish method. *Transactions of the British Mycological Society*, 17, 150–153, doi: 10.1016/S0007-1536(32)80033-1.

Treseder, K.K. & Lennon, J.T. (2015). Fungal Traits That Drive Ecosystem Dynamics on Land. *Microbiology and Molecular Biology Reviews*, 79, 243–262, doi: 10.1128/mmbr.00001-15.

Trinci, A.P.J. (1974). A study of the kinetics of hyphal extension and branch initiation of fungal mycelia. *Journal of General Microbiology*, 81, 225–236, doi: 10.1099/00221287-81-1-225.

Voriskova, J. & Baldrian, P. (2013). Fungal community on decomposing leaf litter undergoes rapid successional changes. *ISME Journal*, 7, 477–486, doi: 10.1038/ismej.2012.116.

Waksman, S.A. (1922). A Method for Counting the Number of Fungi in the Soil. *Journal of bacteriology*, 7, 339–33941.

van der Wal, A., Klein Gunnewiek, P.J.A., Cornelissen, J.H.C., Crowther, T.W. & de Boer, W. (2016). Patterns of natural fungal community assembly during initial decay of coniferous and broadleaf tree logs. *Ecosphere*, 7, e01393, doi: 10.1002/ecs2.1393.

Van der Wal, A., Ottosson, E. & De Boer, W. (2015). Neglected role of fungal community composition in explaining variation in wood decay rates. *Ecology*, 96, 124–133, doi: 10.1890/14-0242.1.

Walters, M.B. & Reich, P.B. (2000). Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology*, 81, 1887–1901, doi: 10.1890/0012-9658(2000)081[1887:SSNSAG]2.0.CO;2.

Weaver, T. & Grime, J.P. (1980). Plant Strategies and Vegetation Processes. *Journal of Range Management*, 33, 159, doi: 10.2307/3898436.

Weichert, M. & Fleißner, A. (2015). Anastomosis and Heterokaryon Formation. In: *Fungal Biology*, Fungal Biology (eds. van den Berg, M.A. & Maruthachalam, K.). Springer International Publishing, Cham, pp. 3–21.

West, G.B., Brown, J.H. & Enquist, B.J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*, 276, 122–126, doi: 10.1126/science.276.5309.122.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002). Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. *Annual Review of Ecology and Systematics*, 33, 125–159, doi: 10.1146/annurev.ecolsys.33.010802.150452.

Wood, J., Tordoff, G.M., Jones, T.H. & Boddy, L. (2006). Reorganization of mycelial networks of Phanerochaete velutina in response to new woody resources and collembola (Folsomia candida) grazing. *Mycological Research*, 110, 985–993, doi: 10.1016/j.mycres.2006.05.013.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., ***et al.*** (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827, doi: 10.1038/nature02403.

Zanne, A.E., Abarenkov, K., Afkhami, M.E., Aguilar-Trigueros, C.A., Bates, S., Bhatnagar, J., ***et al.*** (n.d.). Fungal functional ecology: Bringing a trait-based approach to plant-associated fungi. *Biological Reviews Manuscript*, 1–30, doi: 10.1097/00001888-200003000-00017.

Zeilinger, S., Gupta, V.K., Dahms, T.E.S., Silva, R.N., Singh, H.B., Upadhyay, R.S., ***et al.*** (2016). Friends or foes? Emerging insights from fungal interactions with plants. *FEMS Microbiology Reviews*, 40, 182–207, doi: 10.1093/femsre/fuv045.

Zhang, J. & Elser, J.J. (2017). Carbon: Nitrogen: Phosphorus stoichiometry in fungi: A meta-analysis. *Frontiers in Microbiology*, 8, 1–9, doi: 10.3389/fmicb.2017.01281.